RHIZOME ORGANIZATION IN RELATION TO VEGETATIVE SPREAD IN MEDEOLA VIRGINIANA

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THE INDIAN CUCUMBER, *Medeola virginiana* L., represents the only species of the genus *Medeola* (Trilliaceae). Plants develop above-ground parts and flowers during summer in rich woods, from Quebec south through the Eastern States and down into Florida, Alabama, and Louisiana. Each aërial shoot consists of a single slender stem averaging about 30 cm. in height, bearing two pseudo-whorls of simple leaves and a semi-umbel of small recurved flowers (Fernald, 1950) (FIGURE 1A). The aërial stem arises from an underground rhizome system of great uniformity from plant to plant. This consists of a single thin stem, swollen at its distal end to form a tuber, and normally producing just two branches during the summer, one at each end.

The only detailed study of the morphology of *Medeola* is presented in a paper by Berg (1962), where it is compared with that of *Trillium.* His material from three sites in North America (one of them Harvard Forest) was grown for study in Norway in cold frames. The present investigation is based on plants collected from natural sites and records their pattern of symmetrical growth from one year to the next. This shows a high degree of organization which is related to the method of vegetative spread. These plants showed much less diversity than those collected from Harvard Forest but cultivated in Norway.

Other references to *Medeola* contain scant information about the underground stems of the plants (e.g., Holm, 1925; Ker, 1810) or are concerned solely with taxonomy or cytology (e.g., Gates, 1917; Stewart & Bamford, 1942; Woodard, 1948). The present account confirms Berg's observations on rhizome morphology and is intended to draw attention to the remarkable degree of symmetry in the shoot system which permits a very efficient method of exploiting the substrate.

METHODS

Thirty individual plants were carefully exposed in the leaf litter of Harvard Forest, Massachusetts, 25 on May 14, 1973, and 5 on June 27, 1973. The following data were recorded for each plant.

1. Size and maturity of aërial shoot;
2. Dimensions of parent rhizome system;
3. State and orientation of branches;
4. Presence of injury or disease;
5. Depth of rhizome in soil.

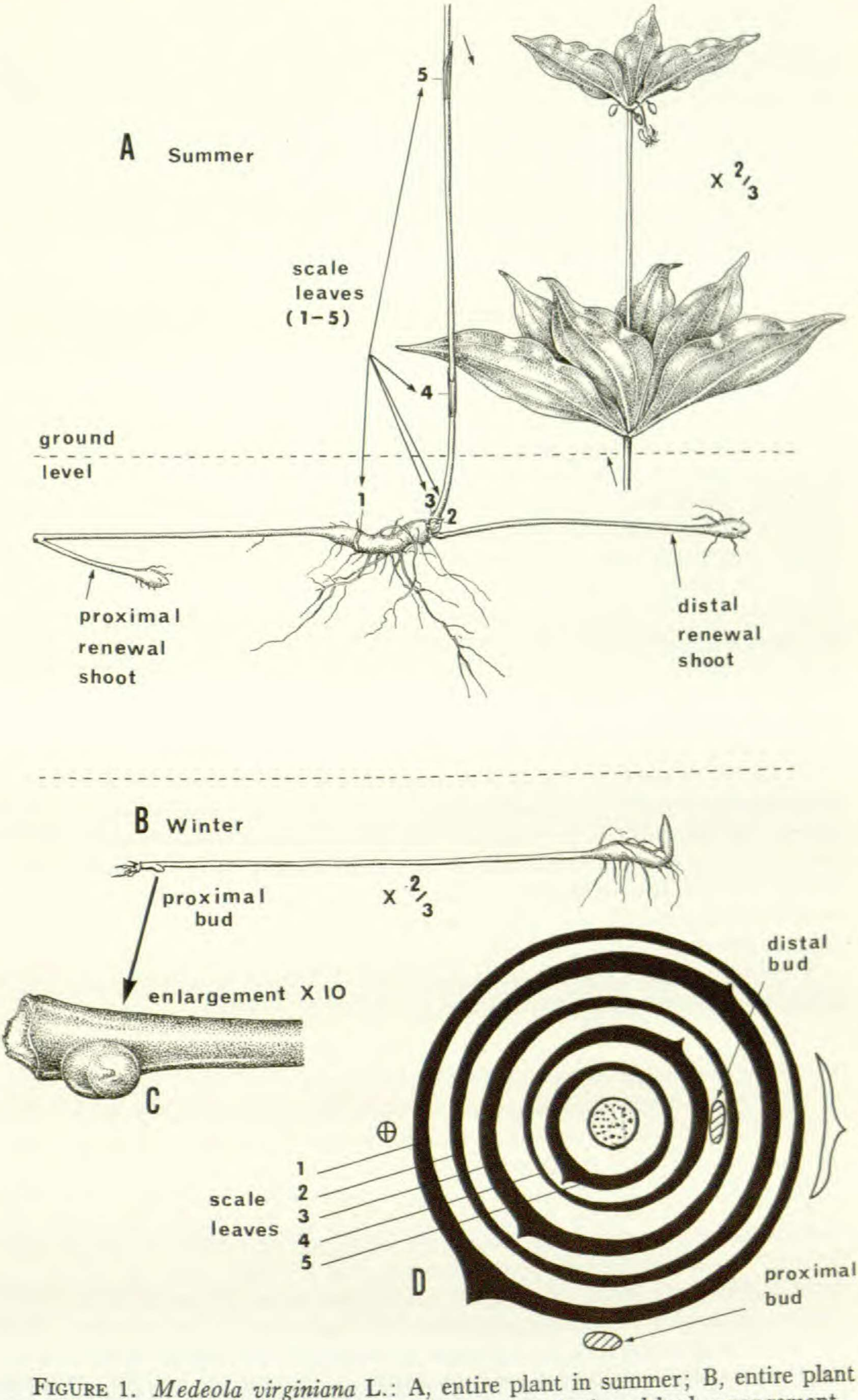

FIGURE 1. *Medeola virginiana* L.: A, entire plant in summer; B, entire plant in winter; C, proximal bud detail; D, plan of scale leaf, and bud, arrangement.

Each plant was located for subsequent study by means of a pair of small flags, and the litter replaced. Unfortunately two thirds of the flags were stolen during the summer. The remaining eleven plants were re-excavated on November 14, 1973. A total of twenty-five plants was fixed in formalin-acetic-alcohol (FAA) during May for further dissection in the laboratory. In addition, five clumps of *Medeola*, each containing about five plants embedded in litter, were transferred undisturbed to a greenhouse in May and excavated in November. Thus this survey is based on the study of about eighty individual plants overall.

OBSERVATIONS

The subterranean part of the plant consists of a long, thin, brittle stem about 3 mm. in diameter bearing neither roots nor leaves for most of its length but terminating in a swollen root-bearing tuber. The distal end of the tuber turns erect to form the aërial shoot. Forward extension of the sympodial system is continued by the development of a single vegetative bud (the distal bud) at the base of the aërial shoot. This is always associated with a scale leaf but is not necessarily opposite its mid-vein. A second vegetative bud (the proximal bud) appears close to the proximal end of the parent rhizome, entirely unconnected with any foliar appendage (FIGURE 1B). Further buds, which normally do not develop, may be present, subtended by other scale leaves. Each unit of the sympodium includes up to two whorls of foliage leaves on the aërial stem, six leaves on average in the lower, and three in the upper whorl. In addition there are five scale leaves, one on the tuber, two at the base of the aërial shoot, and two further up the aërial shoot. These may be numbered for convenience 1–5 (FIGURE 1, A and D). Scale leaf 3 always subtends the distal vegetative bud, except occasionally in small plants which may have only four scale leaves, lacking the one on the tuber (1). Berg (1962) distinguished between scale leaves (recording up to five on the tuber) and cataphylls — three or rarely four associated with the aërial shoot. His diagrams, however, indicate the condition I have recorded, i.e. five reduced leaves in all, with scale leaf 3 subtending the distal renewal shoot.

All plants show a remarkable uniformity of branching pattern despite a considerable range in overall size at maturity as follows:

	Average	*Range*
Height of aërial stem	29.2 cm.	15.0–54.0 cm.
Length of underground stem	11.0 cm.	3.0–27.0 cm.
Length of tuber	3.0 cm.	1.5– 5.0 cm.

Small tubers produce small aërial shoots. Generally speaking, tubers less than 3 cm. long develop aërial shoots with one whorl of leaves and no flowers; tubers greater than 3 cm. long produce two whorls of leaves with flowers. In an established population the size of plants can be related to their position of origin; small plants originate from proximal buds, large plants originate from the distal buds. Similarly the narrow rootless stem section is proportionally much shorter in small plants than in large plants. Rhizomes were found at an average depth in the soil of 5.5 cm., ranging from 3 cm. in compacted soil to 13 cm. in loose litter.

Annual sequence of growth and branching pattern. The dormant plant in late fall is shown in FIGURE 1B. It consists of a swollen distal end bearing roots and terminating in an upturned bud in which all the aërial grains. Scale leaf 3 of the upturned bud has a very small renewal bud in its organs of next year's growth are present. The tuber is packed with starch axil, usually oriented to point forward. The proximal end of the plant consists of the long thin stem bearing neither leaves nor roots. Within 2 to 3 mm. of the blunt end of this narrow stem, to which the remains of the parent axis may be attached, there is a second small bud situated horizontally either to the left or to the right (FIGURE 1C). The origin of this proximal bud is obscure; as was observed by Berg, it is not associated with a leaf. The plant in this winter dormant state is shown diagrammatically in FIGURE 2A.

In the spring (May in Massachusetts), the large upturned bud expands, raising a first whorl of vegetative leaves above the ground. About this time the forward pointing renewal bud grows horizontally through the soil. It bears no roots, and the only leaves are three leaf primordia at its apex. This state is represented diagrammatically in FIGURE 2B. During the summer the horizontal stem continues to extend forward for some 15 to 20 cm. and then its distal end swells, beginning in July. The developing tuber produces roots, thus arresting further growth. During this time also the aërial stem continues to grow, unfolding a second whorl of usually three small foliage leaves and the terminal inflorescence. Towards the end of the summer the proximal vegetative bud grows out horizontally for some 2 to 5 cm. at an angle of approximately 45° to the parent stem, and its advancing end also begins to swell, illustrated diagrammatically in FIGURE 2C. This branch has the same construction as the parent axis, but as has been noted, its dimensions are smaller. In the fall the aërial system dies and withers and the parent rhizome system entirely rots away. A distinct line of separation is developed, producing the blunt but rounded proximal end. Proximal vegetative buds develop on the two daughter plants as shown at *u* and *v* in FIGURE 2D. This sequence is repeated each year, theoretically producing four plants during the second year (FIGURE 2F), eight plants during the third year (FIGURE 3A), and sixteen plants during the fourth year (e.g., by the fifth winter the theoretical population would be represented by FIGURE 3B).

This potential doubling of the population each year in fact must occur very rarely since mortality of individuals during the summer and fall is high. Often the proximal vegetative bud is absent — the rear end of the parent rhizome either becoming rotten, or being eaten, or failing to develop. The same fates sometimes befall distal vegetative buds. In this manner the number of individuals in an area is restricted.

Organization and symmetry. The symmetry of the shoot system is very strict and seems well adapted to exploiting the forest floor. In every excavation in which the disposition of two successive seasons' growth could be determined, the proximal vegetative bud was on alternate sides from one year to the next. If it is on the right one year it will be on the left the next

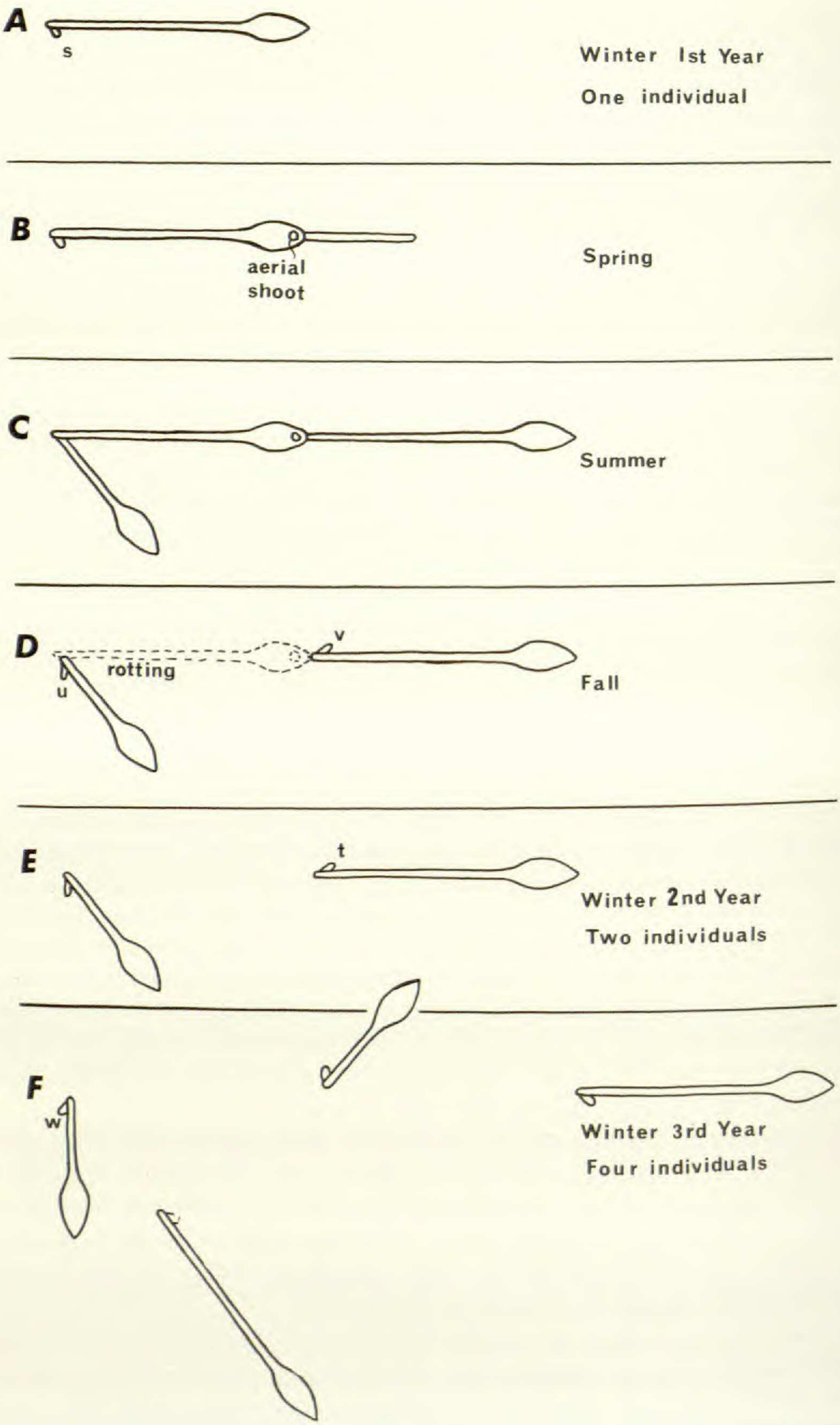

FIGURE 2. *Medeola* branching pattern. Diagrammatic plan view, 1st to 3rd years (s, t, u v, w, see text).

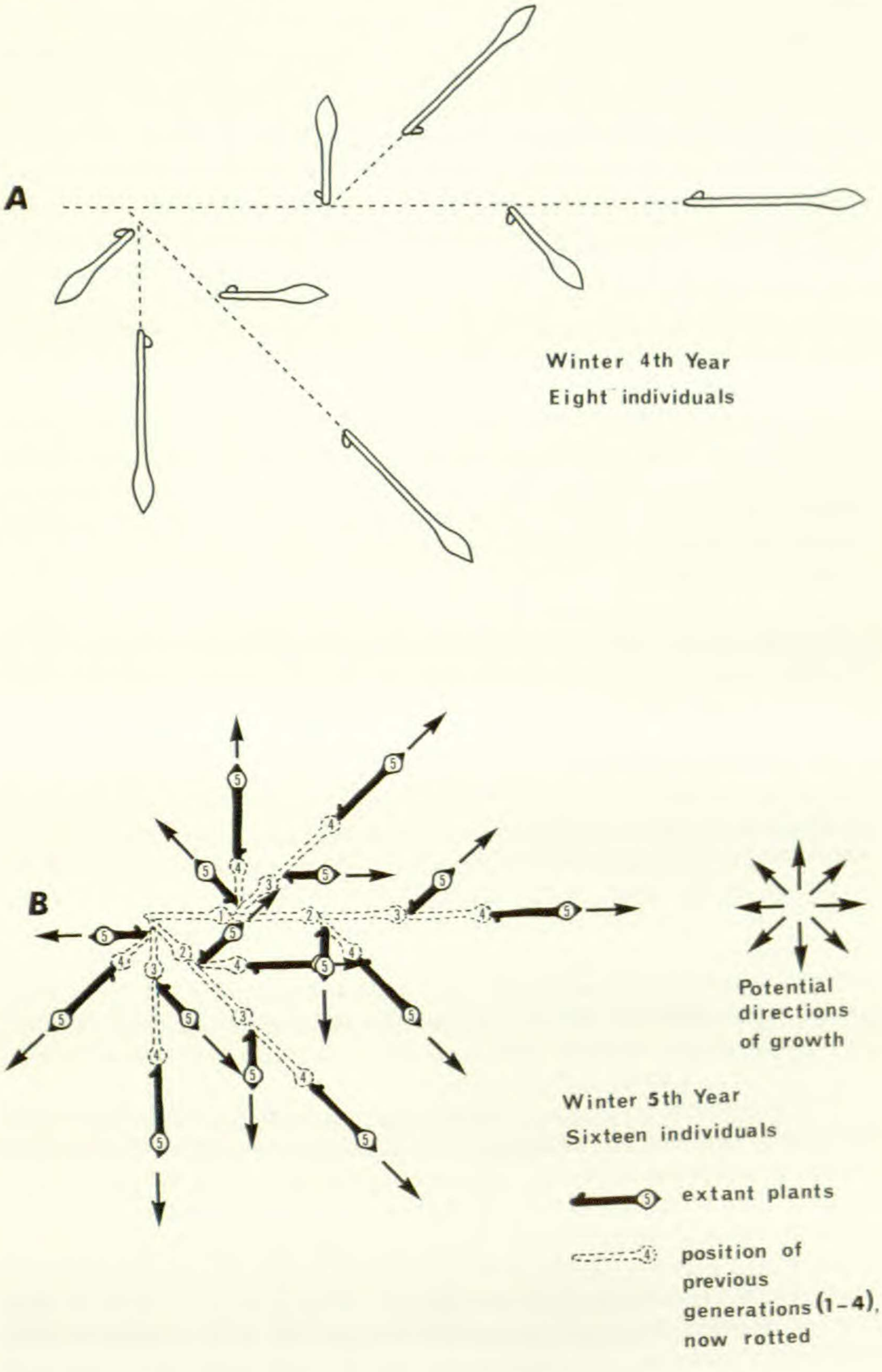

FIGURE 3. *Medeola* branching pattern. Diagrammatic plan view, 4th to 5th years.

year and *vice versa.* This is made evident by comparing FIGURES 2A and 2E; the right-hand bud (*s*) in A is on the left (*t*) in E. No deviations from this rule were found. Consequently as the rhizome system advances forward one unit each year, it leaves behind a second unit alternately to the left and right and thus initiates new lines of growth at 45° to the line of growth of the parent axis. This is evident in FIGURE 3A, where the lines of growth are drawn in. At the same time, the base of each line of growth continues as a generating center for a series of new lines whose orientation rotates 45° each year. The direction of rotation is constant because proximal buds are consistently to the same side — a right hand proximal bud always bears its proximal bud to the right and *vice versa.* Again no deviations from this rule have been observed (c.f. for example the buds *s*, *u*, and *w*, in FIGURE 2). Consequently, at the same time as the rhizome front advances, it leaves behind an increasing number of loci where proximal buds are developed. The appearance of the rhizome system after four years' growth is shown in FIGURE 3B. Sixteen dormant plants (solid black) are present representing lines of advance in eight directions at 45° intervals around the compass. The axes which generated these existing plants are represented in outline.

From an ecological standpoint this rigid organization results in the potential migration of the clone in all directions plus a constant restocking at all sites — the rear buds borne on rear buds rotating portions of the clone on the spot, so to speak.

Leaf orientation. Rather surprisingly the consistent positioning of the vegetative buds does not appear to be governed by a consistent orientation of the scale leaves on the rhizome. The first leaf along the stem (1) is the one borne at about the middle of the tuber. The dorsal side of this leaf may be located at any point on the circumference of the axis of the tuber, apparently at random and without reference to the dorsiventral symmetry of the rhizome. The remaining four scale leaves (2–5) are in a distichous order in relation to the first leaf (1). Again, the distal vegetative bud is positioned towards the advance side of the aërial shoot, in most cases regardless of the dorsiventral and encircling orientation of the subtending scale leaf (3) (FIGURE 1D).

Serial transverse sections reveal that the proximal vegetative bud is not associated with a leaf; nevertheless it inevitably develops in a position which correctly maintains the rigid organizational pattern of the rhizome system. This is one of the most distinctive and remarkable features of this shoot system and presents something of a morphogenetic puzzle.

Growth under greenhouse conditions. Five clumps of *Medeola* were dug up intact in May and maintained undisturbed in a greenhouse with ample light and water for the duration of the growing season. The result of this simple transplantation was quite dramatic and illustrated the further potential for vegetative propagation which is not manifest in natural populations.

Five of these plants are shown diagrammatically in FIGURE 4. The favorable growing conditions have resulted in the production of additional tubers in two ways. Firstly there is the precocious development of shoots which are normally the product of several years' growth, e.g., at *x* in FIGURE 4, where two generations (or orders) of branching develop in one year. Secondly, there is the emergence of branches associated with scale leaves other than scale leaf 3, e.g., at *y* in FIGURE 4. These branches sometimes bear precocious branches themselves, always to the same side consistently either to the left or right and thus behaving like proximal branches in the normal plant, e.g., *z* in FIGURE 4. If a single plant had produced all the variations represented by these five examples, it would have developed nine new plants in the one season compared with the maximum of two produced by a plant in the field.

In view of the results of this simple experiment, it is all the more remarkable that in spite of the potential for extra bud development, vegetative growth is constantly restricted to two buds at opposite ends of the plant.

DISCUSSION

The organized mobility of a clone of *Medeola* described in this account represents a relatively simple example of a widespread phenomenon. A great many plants are rhizomatous (or stoloniferous), only one major group, the Gymnosperms, apparently lacking examples of this ubiquitous mode of growth. However, precise details of rhizomatous growth patterns are infrequently recorded (e.g., N. Hallé, 1967, *Aframomum* and *Costus*; McClure, 1966, bamboos; Primack, 1973, *Lycopodium*; Smirnova, 1967, *Carex* and *Aegopodium*; Takenouchi, 1931, bamboos; Tomlinson, 1970, *Croomia* and *Thalassia*; Tomlinson & Esler, 1973, *Ripogonum*; and *Alpinia*, at present under study, Bell).

It appears that a limited number of basic pattern types reoccur in unrelated groups. *Trientalis borealis* Raf. (Primulaceae) growing in the same habitat as *Medeola* has a similar annual rhizome strategy, producing one (sometimes two) distal renewal shoot but lacking the proximal shoot (Anderson and Loucks, 1973). Invariably the addition of new units to the distal ends of the system is accompanied by the progressive rotting of the old proximal end, resulting in the "movement" of the plant through the soil (c.f. Holttum, 1955; Madison, 1970). *Medeola* is unusual in that an individual never consists of more than three orders of branching at a time — two mature and the third represented by buds, and particularly in that one branch arises at the proximal end of the parent. (A superficially similar sequence occurs in *Costus spectabilis*, which, however, has a vertical two-unit rhizome system; F. Hallé, 1972, personal communication.)

Individual ramets of most rhizomatous plants consist of more than three consecutive orders of branching (a ramet is a single vegetative member of a clone, the genet; Sarukhán & Harper, 1973). The extent of spread of a genet will depend on the details of rhizome pattern and durability.

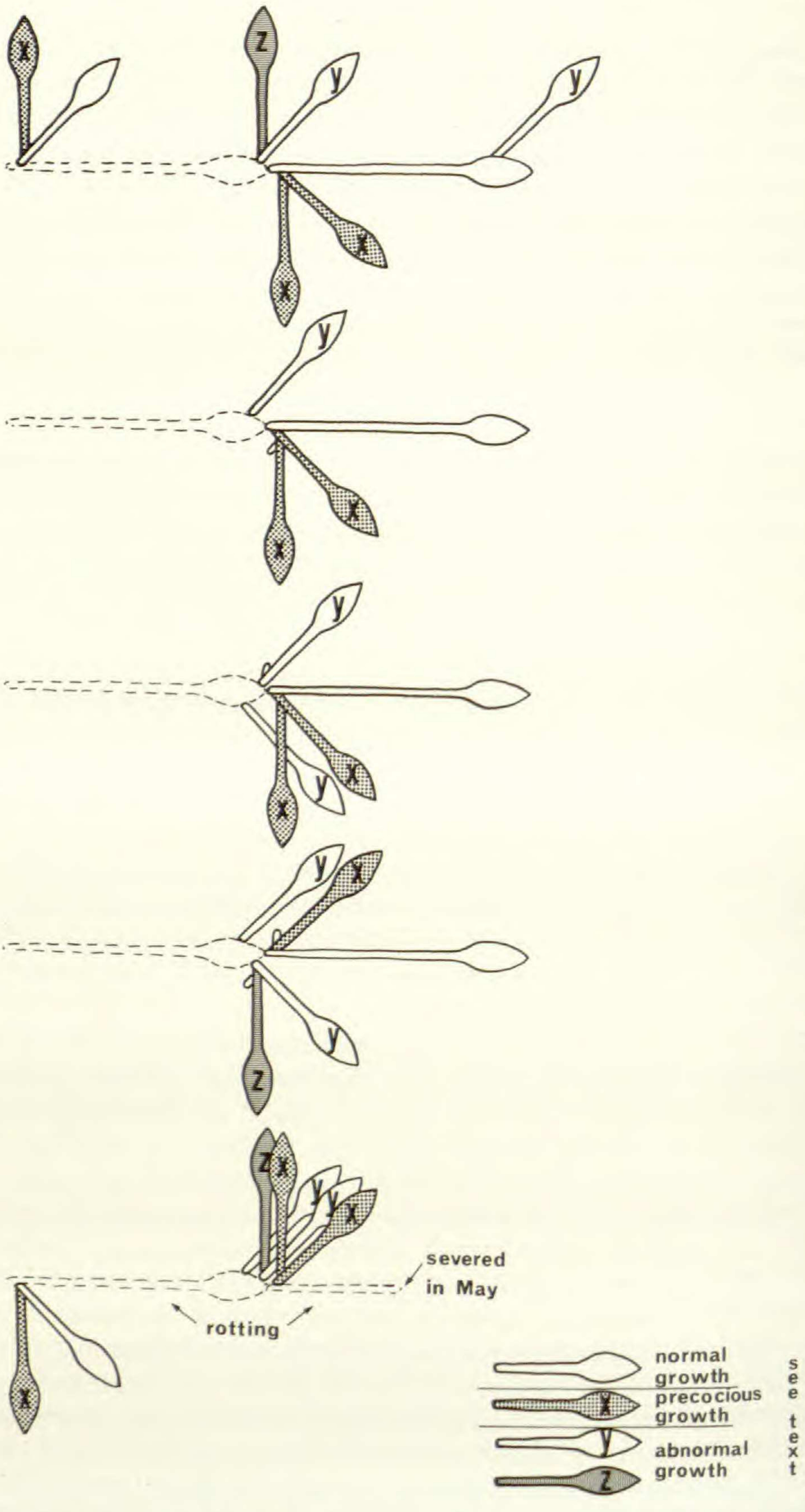

FIGURE 4. *Medeola*. Growth under greenhouse conditions.

The inevitable influence of rhizome symmetry on the location of plants in an ecological context is commonly ignored. It is not usually feasible to excavate an entire plot to determine the subterranean affinities of aërial "individuals," and the significance of the rhizomatous habit in a community is overlooked. However, the symmetrical organization of many of these plants allows quantitative data typifying specific patterns to be collected, and the future growth and spread of the plant can be simulated for many generations. This approach to population dynamics as governed by growth habit is at present being assessed by the author in the case of a ginger, *Alpinia speciosa* (Zingiberaceae). A computer linked to a graphic display screen can demonstrate the future spread of a population given the rules of branching determined by a detailed study of an actual population. The results are proving to be very interesting and allow considerable scope for further study.

SUMMARY

The rhizome of *Medeola virginiana* L. (Trilliaceae) is a simple but highly organized sympodial structure. Under natural growing conditions the rhizomes of individual plants vary in size but not in their quantitative construction. In its winter resting state each long thin rhizome, which is swollen at its distal end, bears five scale leaves and two branch buds. One of these buds (the distal bud) grows horizontally forward from the base of the developing aërial shoot during the following spring. A little later the second (proximal) bud extends horizontally sideways from the extreme proximal end of the parent rhizome and at an angle of 45° to it. This bud does not arise in the axil of a leaf. During the fall the parent unit completely rots away leaving the two dormant branch units now independent of each other. The process is then repeated, the potential annual doubling of the population being modified by a high mortality rate. The symmetrical pattern of events from year to year is recorded. The disposition of the proximal bud follows a very strict sequence alternately from left to right in successive generations. The overall result is a predictable spread of the clone in eight directions from distal buds, together with replacement at each site by proximal buds. The significance of predictable rhizome patterns in population ecology is briefly discussed.

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